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Invited Research Article

Rethinking catastrophe? Historical trajectories and modelled future vegetation change in southern Africa

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ABSTRACT

Most projections of climate change for southern Africa describe a hotter and drier future with catastrophic consequences for the environment and socio-ecological sustainability of the region. This study investigated whether evidence of the projections for the climate and vegetation of the subcontinent is already evident. Analysis of the climate record indicate that the historical trend of increasing temperature is consistent with future projections for the region. Rainfall, however, apparently has not changed significantly. Results from analysis of 1321 repeat historical photographs indicate broad trends in vegetation trajectories in the major biomes of southern Africa. The Savanna biome has experienced a rapid increase in woody plant at rates un-anticipated by the models. Contrary to early projections for the Succulent Karoo biome, biomass and cover have increased, largely in response to changes in land-use practices. Cover in the fire-adapted Fynbos biome has remained stable or increased over time with unanticipated expansion of forest species, particularly in localities protected from fire for long periods. The shrub-dominated Nama-karoo biome has increased in grass cover. Rather than contracting, as suggested in the early models, the Grassland biome has apparently expanded westwards into former Nama-karoo biome sites. The Savanna biome has experienced a rapid increase in woody plants at rates not anticipated by the models. The broad trends in historical trajectories illustrate how land-use management has influenced vegetation change in the past. They also provide a useful context for evaluating future changes and developing mitigation strategies for some of the worst impacts of climate change in the future.

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1. Introduction

For decades, climate scientists have analysed historical trends in regional and global temperatures and compared them to simulated values derived from mechanistic models of climate. The scientific consensus that has arisen from this effort is that current climate warming can largely be attributed to anthropogenic emissions of greenhouse gases (Bindoff et al., 2013). A warming climate has obvious implications for the biological world and numerous studies have documented range shifts in species or local extinctions, particularly in the northern hemisphere, where more long-term records are available (Lenoir and Svenning 2015; Wiens, 2016). The rapid development of global climate models and the projection of future climate impacts on the environment have also had a significant influence on a wide range of national and global policies that affect the way society uses energy, consumes natural resources, and prepares for a more sustainable future (DEA, 2011; IPCC, 2014; United Nations, 2016).

However, future projections on their own provide insufficient justification for large-scale interventions in the way society functions and uses resources. Projected future trends in climate and greenhouse gas concentrations, and their likely impacts on the environment, should also be viewed in light of historical trends in the environment. Changes to the environment, that have occurred in the past century or more, allow the effect of known changes in climate and greenhouse gases to be examined more closely (Tillman et al., 2017). The degree of continuity between historical changes in the environment and projected trends will also affect the confidence that society has in future projections. Greater reconciliation and integration of findings from palaeoecological studies, historical observations, satellite-based remote sensing products and models is needed to build a stronger, evidence-based, policy framework (Costanza et al., 2012).

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In this contribution, which focuses on South Africa and southern Namibia, we highlight the importance of an historical perspective in global change research and policy formulation. We first describe the development of the climate change narrative in the region and summarize the historical evidence for this. We then review the generally catastrophic impacts that future climate change is projected to have on southern Africa. From this we derive a set of hypotheses for each of the major biomes in the region which clarify the expected trajectories of change in a warming world. Next, drawing on an analysis of 1321 repeat photographs, we document the long-term historical trends in vegetation within each of the major biomes of the region with a focus on vegetation cover, and the switch in dominance of different plant growth forms. Areas of agreement and disagreement between future projections and historical trajectories within each of the major biomes are identified. Four potential reasons for a lack of consensus between future projections and some historical trajectories are proposed. We conclude that long-term trends measured in the historical record provide an important baseline against which future scenarios can be evaluated. They also provide an assessment of the relative influence that climate and land-use have on vegetation change.

2. Future and historical climate change projections for southern Africa

For southern Africa, most climate scenarios for the 21st century project a hotter future for the subcontinent (Tadross et al., 2011; UK Met Office, 2011). For example, Engelbrecht et al. (2015) have suggested that relative to the period 1961–1990, annual average surface temperatures for the African sub-tropics, including southern Africa, will range between 4–6 °C higher for the period 2071-2100. Projected changes in rainfall for the sub-continent also indicate a drying trend with an expansion of Köppen-Geiger's hot desert and hot steppe climate zones into the more temperate cooler zones of southern Africa (Engelbrecht and Engelbrecht, 2016). For summer season precipitation, comparisons between an ensemble of 15 GCMs and two downscaling techniques (statistical and dynamical) are contradictory, although a decrease in rainfall for western southern Africa is generally indicated (Shongwe et al., 2009; Haensler et al., 2011; Gizaw and Gan, 2017). The biodiverse, winter rainfall region, in particular, is expected to be significantly drier as a result of the southward contraction of the mid-latitude belt of westerly winds in the southern ocean (Tadross et al., 2011) although some downscaled climate models indicate smaller impacts than previously suggested (Driver et al., 2012). Clearly, the complexity of the processes and physical mechanisms involved in determining southern Africa's climate, including the influence of the El Nino-Southern Oscillation (ENSO) and sea surface temperature (SST), make it extremely difficult to predict future trends from global climate models (Masih et al., 2014).

Most analyses of historical climate data sets for southern Africa show broad coherence with the expected changes in climate and indicate that both maximum and minimum temperature has indeed increased over the course of the 20th century for most locations within the sub-continent (Hoffman et al., 2011; MacKellar et al., 2014; Engelbrecht et al., 2015; Davis et al., 2016). There is less agreement over the extent and direction of change in annual rainfall totals, with most studies suggesting that long-term trends in rainfall have not been significant (Tadross et al., 2011; MacKellar et al., 2014). Despite this, there is some evidence that the frequency, intensity and extent of drought over the last 50 years has increased over much of the African continent including southern Africa (Rouault and Richard, 2003; Masih et al., 2014). However, an analysis of a longer rainfall time series for South Africa suggests that severe to extreme drought conditions prevailed over nearly 50% of South Africa in 1933 and 1949 (Malherbe et al., 2016) and that drought has been a regular feature of the southern African region for centuries (Ballard, 1986). While the severe drought experienced in the summer rainfall region of South Africa in 2013/15, and the even more extreme 2015/17 drought in the winter rainfall region (Botai et al., 2017) have yet to be fully assessed, their occurrence has exacerbated concerns about the likely future impacts of climate change-related drought incidence on the sub-continent.

As important as temperature and rainfall are for plant growth and the proper functioning of natural ecosystems, other climate variables such as wind, solar radiation, relative humidity and evaporation also influence whole plant physiology through their impact on water stress. Despite the measured increase in

Table 1
The projected impacts of future climate change on different components of southern African ecosystems.

Component of the ecosystem affected	Location	Description of the projected change	Source
Vegetation	Southern Africa, Savanna, Grassland biomes	Large increase in woody plant cover mostly in response to an increase in CO_2; expansion of forest, woodland and savanna and contraction of grassland biomes.	Moncrieff et al. (2015); Higgins and Scheiter (2012)
Water, vegetation, animals	Southern Africa	Reduction in surface water flow, increase in woody cover in summer rainfall areas with concomitant impact on faunal diversity; loss of biodiversity in winter rainfall region.	Midgley and Thuiller (2011)
Vegetation, endemic plants	South Africa, Succulent Karoo biome	Significant loss of bioclimatically-suitable surface area for succulent Karoo biome species and significant reduction in range size by 2050 for 17 of 20 endemic species modelled.	Midgley and Thuiller (2007)
Vegetation, endemic plants	Southern Africa	Habitat-specific species richness could be reduced by up to 40%.	Broennimann et al. (2006)
Water, vegetation, health	South Africa, Western Cape	Degradation of rivers, wetlands and estuaries as a result of desiccation, up to 40% increase in high fire risk conditions, up to 30% loss of species in Fynbos and Succulent Karoo biomes, increase in air pollution and heat stress, increased risk of economic loss from flooding and asset losses, negative impacts on agricultural production.	Midgley et al. (2005a)
Vegetation, endemic plants	Namibia	Desert and Arid shrubland will expand into Grassy Savanna, reduction in cover and Net Primary Production (NPP); increase in fire frequency and intensity, in some scenarios over 30% of the 800 species modelled projected to become Critically Endangered or Extinct in Namibia by 2080.	Midgley et al. (2005b)
Endemic plant family (Proteaceae)	South Africa, Cape Floristic Region	Depending on the climate change and land use scenario, up to a third of the 227 Proteaceae species investigated uplist their IUCN Red List conservation status (i.e. become more threatened) and 2% become Extinct because of climate change.	Bomhard et al. (2005)
Dune mobility	Central southern Africa	Reduction in vegetation cover and soil moisture, increase in wind energy leading to a re-mobilization of Kalahari dune fields.	Thomas et al. (2005)

temperature, pan evaporation (a measure of actual evaporative demand) has declined in some areas of South Africa including the Nama-Karoo biome (Eamus and Palmer, 2007) and the winter rainfall region of the southwestern Cape (Hoffman et al., 2011). This 'evaporation paradox' is a global phenomenon and, as is the case in the southwestern Cape, appears linked to a decline in wind speed and, in some cases, solar radiation, over global terrestrial environments in recent decades (McVicar et al., 2012; Breña-Naranjo et al., 2017). The inclusion of wind speed as a dynamic function in indices of drought severity such as the Palmer Drought Severity Index (PDSI) has a significant impact on the extent of drought recorded for a region or continent over time. For example, Sheffield et al., (2012) showed for the United States how the inclusion of other factors in the PDSI which influence the hydrological cycle such as solar radiation, wind speed and humidity reduced the extent of drought in the USA to one seventh the area previously recorded and led them to conclude that drought has not changed significantly over the last 60 years. These results affect the way in which the response of the terrestrial environment to global warming should be interpreted (McMahon et al., 2013).

3. The expected impact of climate change on biodiversity and the environment

Most studies on the future impacts of climate change in southern Africa focus on changes in vegetation, biodiversity and ecosystem function (Midgley and Thuiller, 2011) (Table 1). For example, results from the first bioclimatic envelope models for the region (Midgley et al., 2000) suggested that all biomes in South Africa will contract in a warmer future with large areas in the semi-arid and arid west becoming so dry that no current vegetation type analogue could occupy such an arid region. These projections suggested that the biodiverse Succulent Karoo biome will be affected the most since, by 2080, optimal bioclimatic habitat is projected to contract by up to 65% (Midgley and Thuiller, 2007). Similarly, for Namibia, bioclimatic envelope models suggested an expansion of the desert and arid shrublands by about 30% into present grassy savannas by 2080 with an associated loss of vegetation cover and Net Primary Production (NPP). It is proposed that this will result in the contraction in the distribution of about 30% of the 800 species modelled (Midgley et al., 2005b) including many endemic species (Thuiller et al., 2006). The associated impact of climate change on Namibia's agricultural and fishing outputs is projected to reduce the country's GDP over 20 years by between 1 and 6% with the unskilled labour sector being the most affected (Reid et al., 2007). Other impacts of climate change projected for southern Africa include the widespread remobilization of the large Kalahari dune fields in response to reductions in vegetation cover and moisture availability and increases in wind energy (Thomas et al., 2005).

More recent models of how southern African vegetation might respond to climate change in the 21st century are substantially different in their outcomes from those developed earlier and reflect an evolving narrative about climate change impacts in the region. Driver et al., (2012) used more recent climate data from 15 GCMs which were statistically downscaled to develop biome distribution models under three climate scenarios (best case, intermediate and worst case). Their projections for South Africa's biomes to 2050 show that, in contrast to earlier models, the Succulent Karoo biome will be least affected by climate change. Similarly, the likely impact of climate change on the Fynbos biome has also been substantially revised with the northern and eastern areas of the biome being most affected. Only up-slope altitudinal shifts in suitable climate envelopes are now suggested for the core southwestern mountainous areas of this biome. These differences with previous projections are because statistical downscaling returns substantially smaller impacts on the winter rainfall climate than previously suggested.

However, even in these revised projections, the Grassland biome remains under significant threat from climate change and could retreat to the areas of highest altitude under the worst case scenario while the Desert biome will likely expand into the Nama-karoo biome, particularly under conditions of greatest water stress (Driver et al., 2012). Even without the inclusion of rising levels of atmospheric CO_2, which has been proposed as a key driver of woody plant increase in mesic parts of South Africa (Wigley et al., 2010; Higgins and Scheiter, 2012), a significant expansion of climatically-suitable areas for the Savanna biome is likely in the future. Driver et al., (2012), however, emphasize both the uncertainties associated with the 'downscaled' climate projections at regional and local levels as well as the uncertainties associated with species and ecosystem responses to the new climate envelopes.

Using a different approach from the earlier climate-only, niche-based models, Higgins and Scheiter (2012) have developed an adaptive Dynamic Global Vegetation Model (aDGVM) to demonstrate how the abundance of savanna trees, forest trees and C_4 and C_3 grasses are likely to change across the African continent over the 21st century in response to increasing temperature and atmospheric CO_2 concentrations. Rainfall remained at ambient levels and land use impacts were ignored in the model. Their results suggest that the grassland, savanna and forest ecosystems of tropical and subtropical regions, including southern Africa, will be characterized by increased woody-plant dominance and/or higher plant biomass in the future. This directional response is based largely on the leaf-level physiological response to CO_2 concentration and temperature increase which favours growth forms with C_3 photosynthetic types, such as trees, over C_4 grasses. Moncrieff et al., (2015) used a similar modelling approach to predicting the distribution of South African biomes in 1900, 2012 and 2100. Output from their model also points to a significant increase in woody plant cover and an expansion of woodland and forest biomes, largely at the expense of grasslands. However, this increase is only apparent in the time step from 2012 to 2100 as little change is evident for the initial period covered by the model from 1900-2012. Midgley and Bond (2015) also point to the important role of CO_2 in counteracting the effect of climate-related aridification, particularly for southern Africa's arid and semi-arid regions. In contrast to earlier projections they suggest that, because water use efficiency of the dominant growth forms will increase under rising CO_2

Table 2
The percent of repeat photographs scored in each of five Vegetation Cover Change Index classes when compared against the original photograph in eight southern African biomes. The index values reflect the percent change in vegetation cover within the following broad classes: −2 = >25% decrease in cover in the repeat photograph when compared against the original; −1 = >5% to 25% decrease in cover; 0 = −5% to +5% difference in cover; +1 = >5% to 25% increase in cover; and +2 = >25% increase in vegetation cover.

Biome	No. comparisons (N = 1529)	Vegetation Cover Change Index				
		−2	−1	0	1	2
Desert	117	1	11	73	14	1
Succulent Karoo	258	3	8	52	28	9
Nama-Karoo	226	1	6	46	35	12
Fynbos	336	4	14	50	24	8
Grassland	323	0	4	45	35	16
Savanna	193	1	4	18	35	42
Albany Thicket	30	7	0	27	43	23
Indian Ocean Coastal Belt	46	2	4	46	39	9
Average		2	8	46	30	14

concentrations, net primary production and plant cover could, therefore, also increase in the arid zone.

4. Comparison of historical trajectories and future predictions of vegetation change

One approach to increasing confidence in future predicted climate and its impacts is to compare future projections with recorded historical data from the whole of the twentieth century. Repeat photography is a powerful tool that allows long-term changes in vegetation change to be studied retrospectively at decadal time-scales (Webb et al., 2010). Here, we compare modelled future projection of vegetation change with historical trends observed in 1321 repeat photographs from eight biomes (Mucina and Rutherford, 2006) in southern Namibia and South Africa. Following the approach of Rohde and Hoffman (2012) each pair of photographs was assessed in terms of the change in vegetation cover within three generalised land forms (plains, slopes and rivers). As some images contained more than one landform, a total of 1529 separate comparisons between the original and repeat photograph were made. The change in cover was assessed according to the same five-point Vegetation Cover Change Index used by Hoffman and Rohde (2011) as follows: −2 = >25% decrease in vegetation cover in the repeat photograph when compared against the original; −1 = >5% to 25% decrease in cover; 0 = −5% to +5% difference in cover; +1 = >5% to 25% increase in cover; and +2 = >25% increase in vegetation cover. The number of photographs within each of the Vegetation Cover Change Index values was calculated for each of the land forms and summed for the biome. This summed value was then expressed as a percentage of the total number of comparisons made for each biome. This assessment provides a broad overview of the extent and direction of vegetation change in each biome over time (Table 2).

A common finding in this analysis is that vegetation in the southern African region has either remained stable over time or has generally increased in cover and biomass over the course of the 20th century. In less than 10% of the comparisons made did vegetation cover decline by 5% or more. Attribution of causality has been much more difficult to establish but both local drivers (e.g. reduction in grazing intensity and fire) and global drivers (e.g. increase in temperature and CO_2) are indicated. Observed decreases in vegetation cover and biomass, however, are usually always associated with the effects of intense human disturbance such as mining, cultivation or wood harvesting. In the case of the Fynbos biome, recent fire is usually responsible for the decrease observed in the repeat photograph. Further details relating to some of the major regions and biomes in southern Africa are discussed below.

4.1. Southern Namibia

Future climate change projections for the region suggest that over the course of the 21st century Desert and Arid shrublands will expand into Grassy Savanna vegetation, with a concomitant loss of vegetation cover and NPP (Midgley et al., 2005b). However, in the arid and semi-arid parts of southern Namibia a 133 year photographic record indicates that there has been very little

Fig. 1. Bucharos Crater, southern Namibia (No. 489). Nama-karoo biome. The foreground vegetation is dominated by *Rhigozum trichotomum* and appears to have changed little over the 133 year period of observation. There has been a slight increase in cover of *Acacia mellifera* and *Cataophractes alexandrii* along the drainage line in the middle distance. [A (top): Coates Palgrave, 28 November 1876; B (bottom): Rohde and Hoffman, 27 August 2008].

change in the cover and composition of key vegetation types (Rohde and Hoffman, 2012) (Fig. 1). In several instances, individuals of the same long-lived tree or shrub species, such as *Acacia erioloba* or *A. hebeclada*, which were evident in the photographs of 1876, were still present when the photographs were repeated in 2009. However, for sites which received more than 275 mm of annual rainfall there has been a significant increase in vegetation cover and biomass, primarily of the dominant woody encroacher species such as *Acacia mellifera* and *Dichrostachys cinerea* (Fig. 2).

4.2. Succulent Karoo biome

Widely divergent projections exist for the Succulent Karoo biome depending on the model parameterization and climate scenarios used. Early projections described substantial contraction of a vulnerable biome resulting in no-analogue communities (Midgley et al., 2000) while recent models suggest that the biome will be resilient to climate change and will not differ substantially in the future from its current distribution (Driver et al., 2012). An analysis of 258 repeat ground photographs suggests, however, that vegetation has generally increased in cover (Hoffman and Rohde, 2007, 2011). The reduction in livestock numbers as well as the decline in the area cultivated has been an important influence on this pattern, which has differed between communally-used and privately-owned parts of the region. Riverine areas in particular have shown an increase in cover, largely of the 3–5 m tall tree, *Acacia karroo*. The few repeat photographs of the ecotone between the Succulent Karoo and the Nama-karoo biomes also suggests an increase in cover, but of C_4 grasses within the genus *Stipagrostis* (Hongslo et al., 2009) (Fig. 3). In contrast to the predictions from both the niche-based, climate-

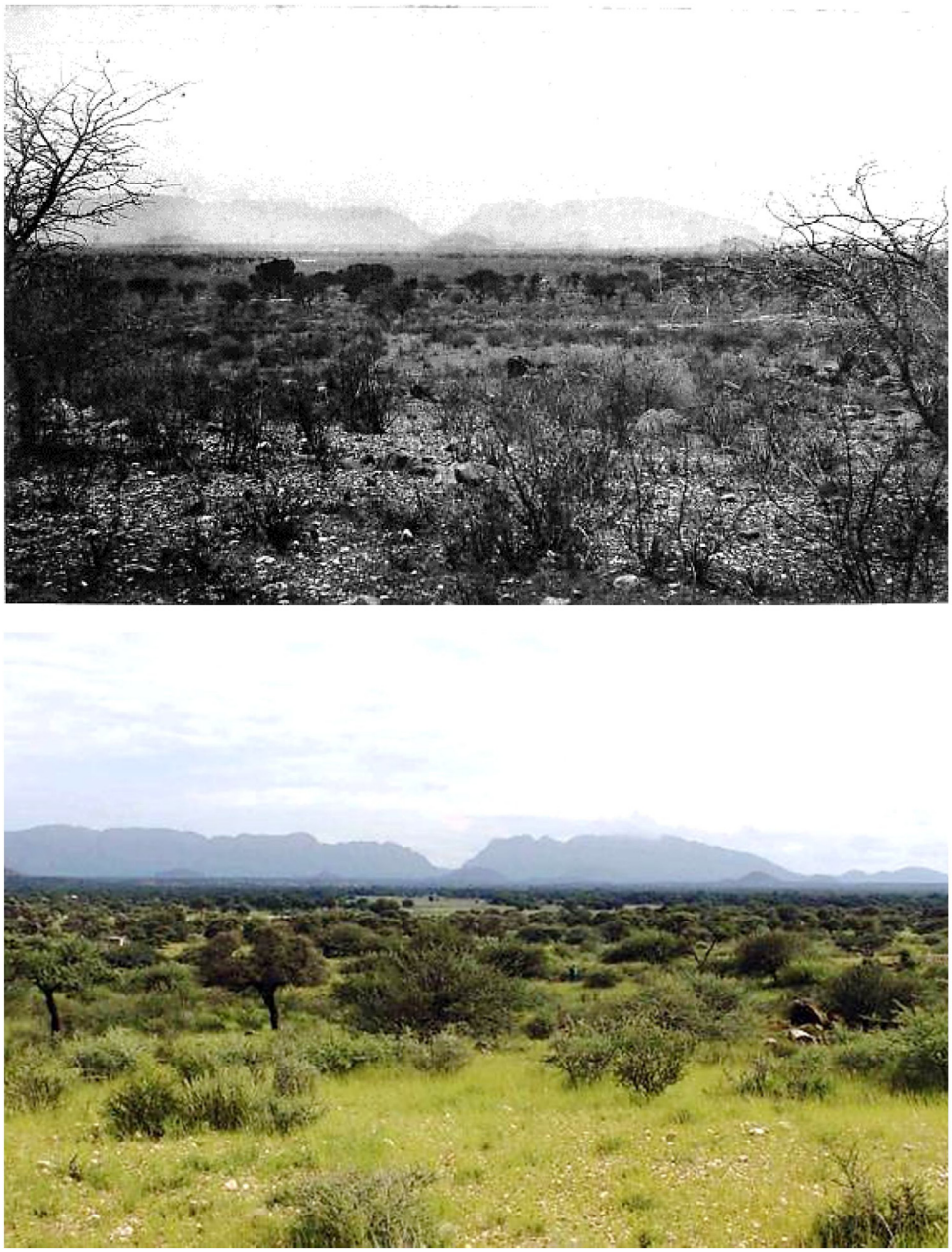

Fig. 2. Geluk Oos, central Namibia (No. 505). Savanna biome. Despite the presence of several homesteads in the field of view, there has been a significant increase in cover of tall shrubs such as *Rhigozum trichotomum* and *Acacia hebeclada* and trees such as *Acacia erioloba* and *Ziziphus mucronata* particularly along the river terrace in the mid-ground. [A (top): Coates Palgrave, 13 October 1876; B (bottom): Rohde and Hoffman 25 February 2009].

Fig. 3. Moreskadu, near Aggenys (No. 370). Desert biome. The original dominance of annuals in the distance and sparse shrubs in the foreground has now changed to a grassland dominated by the grasses *Stipagrostis ciliata* and *S. obtusa* and the leaf succulent shrubs *Eberlanzia ferox* and *Ruschia muricata*. [A (top): Herre, September 1939; B (bottom): Rohde and Hoffman, 20 March 2005].

only models as well as the Dynamic Vegetation Models, there is no suggestion from this evidence that the more arid Desert biome to the north and east has expanded its range into the Succulent Karoo biome over the last 50 years. Increased productivity and an increase in the length of the growing season appear widespread across the region as reported by Davis et al., (2017) in their remote sensing analysis of Namaqualand.

4.3. Fynbos biome and associated forest vegetation

The early catastrophic projections (Midgley et al., 2000; Bomhard et al., 2005) for the winter rainfall Fynbos biome have also been revised (Driver et al., 2012). This biome is now perceived as being amongst the least affected by climate change except at the northern and eastern margins of its current distribution (Driver et al., 2012). Evidence to date is contradictory. For example, Thuiller et al. (2007) documented species changes in 81, 10 x 5 m plots between 1966 and 1996 at the Cape of Good Hope Reserve. While there were important changes in species composition at the local scale, with 74% of the plots exhibiting >50% turnover, there was considerable stability at the 'meta-community' level. Evidence from 78 repeat photograph pairs taken between 1966 and 2012 supports this view of long-term stability within the vegetation of the area (Powell, 2013) (Fig. 4). Most of the changes in growth form and total vegetation cover observed in the repeat photograph pairs could be interpreted in terms of the difference in post-fire vegetation age. There was no evidence of an aridification of the landscape, exemplified by a loss of cover and shift to more arid-adapted growth forms and species, despite the significant increase in maximum temperature apparent in the historical climate record for Cape Point. Populations of emergent Proteaceae shrubs (*Mimetes fimbriifolius* and *Leucospermum conocarpodendron*) had also not declined in abundance since 1966. Contrary to the dramatic changes predicted by early models for the Fynbos biome, it appears remarkably resilient to the changes in the climate experienced so far. However, Slingsby et al. (2017) have recently examined a subset of the data analysed by Thuiller et al. (2007) but over a slightly longer time series. In contrast to the earlier conclusions, they found that high temperatures and drought in the immediate post-fire environment of fynbos ecosystems reduced diversity and had significant negative impacts on resprouting plants, including graminoid and herbaceous growth forms.

One of the most striking changes that has occurred within other parts of the Cape Peninsula has been the increase in Afromontane forest cover over the last 100 years (Poulsen and Hoffman, 2015). Photographs from the late 19th century and early 20th century indicate that forest species were confined to small, relatively isolated patches or to the relatively narrow stream courses on the slopes of mountains (Fig. 5). While not all forest patches have increased in cover there has been a dramatic expansion of forest precursor species such as *Phylica buxifolia* and *Kiggelaria africana* into areas that were previously covered with graminoid and restioid fynbos species in particular. Despite evidence that average fire return intervals on the Cape Peninsula have decreased in the last 30 years, from one every 31.6 years to one every 13.5 years (Forsyth and van Wilgen, 2008), they appear to be far less frequent than was the case in the 19th century, when fire frequencies were of the order of 1–3 years, with devastating consequences for both forests and taller ericoid and proteoid growth forms (Pillans, 1926). In contrast to the expectations, forests on the Cape Peninsula, at least, appear to be recovering from the impacts of past over-exploitation and are expanding their range.

4.4. Grassland and Nama-karoo biomes

The broad ecotone between the Grassland and Nama-karoo biomes has long been a focus in the South African degradation debate. John Acocks' assertion in 1953 (Acocks, 1953) that unpalatable dwarf karroid shrubs were expanding into the sweet grassveld of the Highveld plateau galvanised action within the Department of Agriculture and led to several successful government initiatives to reduce stock numbers and prevent soil erosion in the region (Hoffman and Ashwell, 2001). The vulnerability of the Grassland biome continues to be foregrounded in the climate change literature, which has consistently pointed to this biome as amongst the most threatened in South Africa (Driver et al., 2012). Projections suggest that not only will the suitable climate envelope shrink under a warming subcontinent but the biome will also come under threat from an expansion of woody savanna trees primarily as a result of increased temperatures and CO_2 concentrations in the atmosphere (Higgins and Scheiter, 2012; Moncrieff et al., 2015).

The few long-term data which document vegetation change in the Grassland biome suggest that woody elements within genera such as *Acacia* and *Rhus* have indeed increased in density over the last fifty years but this increase is not spread uniformly across the landscape. Rocky slopes and especially ephemeral streams appear to have shown the greatest increase in trees and tall shrubs over this period (Masubelele et al., 2015). Plains environments appear not to have been invaded by trees and shrubs to the same extent.

Fig. 4. Krom Rivier Sandpit, Cape Point (No. 753). Fynbos biome. There is very little difference in cover and growth form composition between the two photographs although the burnt skeletons of *Leucadendron laureolum* shrubs in the foreground emphasize the difficulty of interpreting long-term change in these fire-driven landscapes. [A (top): Taylor, 1966; B (bottom): Powell and Hoffman, 30 August 2011].

What is noticeable on the plains is the reduction in dwarf shrubs and the increase in tall bunch grasses, such as *Themeda triandra* and *Cymbopogon plurinodis*. At some higher altitude sites, karroid shrublands dominated by dwarf shrubs, such as *Pentzia incana* and *Eriocephalus* spp., have been completely transformed over the last 50 years and are now dominated by the widespread C_3 tussock grass *Danthonia disticha*. Even in the more arid parts of the ecotone, such as near Middelburg, a shift from karroid shrubland to grassland vegetation has occurred (Fig. 6). This extensive westward expansion of grassland species into karroid shrubland runs counter to the bioclimatic envelope model projections (Driver et al., 2012). However, it supports some of the results from the DGVMs which include rising CO_2 as an important driver of growth form change in the more arid parts of the continent (Midgley and Bond, 2015). Current explanations for these shifts, however, suggest that changes in stocking rates over the last 50 years (Masubelele et al., 2014; Hoffman et al., 2018) as well as a significant increase in early summer rainfall (du Toit and O'Connor, 2014) could also account for the increase in grass cover evident in the region.

4.5. Savanna biome

The increase of woody plants within southern African savannas has been well-documented (Skowno et al., 2017). What is surprising is the relatively high rate of increase in woody plant cover as well as the timing of such increase. For example, in 23 of the 24 studies reviewed by O'Connor et al. (2014) the mean increase in woody plant cover was 6.2% per decade and ranged from 2.8% to 29.0%. In the remaining site, located in the Kruger National Park, woody plant cover decreased, purportedly as a result of the impact of elephants. Projections derived from Dynamic Vegetation Models suggest that major increases are likely to occur during the course of the 21st century (Higgins and

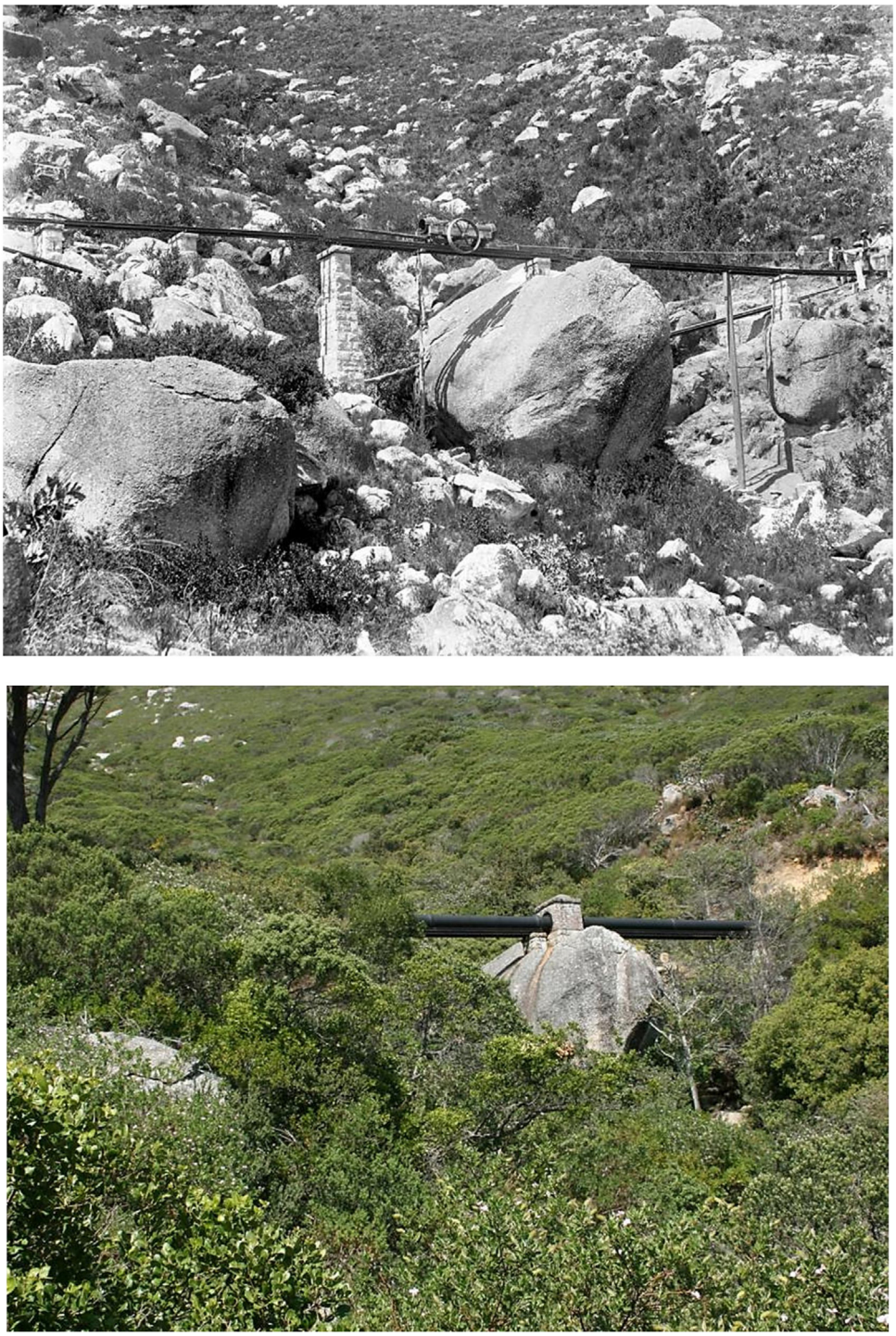

Fig. 5. Kasteelpoort Stream, Cape Peninsula (No. 769). Fynbos biome. There has been a significant increase in Afromontane forest precursor species such as *Phylica buxifolia*, *Kiggelaria africana* and *Rapanea melanophloeos* with a concomitant decrease in low-growing fynbos species. [A (top): Cairncross, 1887; B (bottom): Hoffman, 17 September 2011].

Scheiter, 2012; Moncrieff et al., 2015). However, what the DVMs do not reveal is the significant amount of woody thickening that occurred across the sub-continent during the second half of the 20th century (O'Connor et al., 2014). Future projections, therefore, will relate more to the expansion of woody elements into Grassland biome environments rather than to the changes within existing savannas, which have already been transformed significantly.

The increase in atmospheric CO_2 concentration has been strongly promoted as a cause for woody plant increase in both the DVMs (Higgins and Scheiter, 2012; Moncrieff et al., 2015) as well as in the few experiments carried out (Kgope et al., 2010; Buitenwerf et al., 2012). The role of rainfall, temperature increase, and land use (including fire and herbivory), has also not been ignored (Wigley et al., 2010; O'Connor et al., 2014). For example, much of the historical increase in woody plants has been associated with the high rainfall of the 1970s (O'Connor et al., 2014). Evidence from long-term repeat photographs (Hoffman and O'Connor, 1999, Fig. 7) also shows how quickly woody trees can

Fig. 6. Groenefontein, near Middelburg (No. 10). Nama-karoo biome. There has been a significant decline in the cover of dwarf karoo shrubs such as *Pentzia globosa* and *Eriocephalus spinescens* and an increase in grass cover comprised mainly of *Eragrostis lehmanniana* and *Tragus koelerioides*. [A (top): Roux 1968; B (bottom): Masubelele and Hoffman, 22 January 2009].

colonize abandoned fields (Shackleton et al., 2013). This highlights the importance of past and present land use as an important driver of vegetation change. Exactly how local and global drivers interact to promote woody plant thickening remains a subject of investigation.

4.6. Changes in species distributions

Few examples exist of the impact of global warming on the distribution of southern hemisphere organisms. One exception is *Aloe dichotoma*, a 5 m tall arborescent succulent tree distributed within the drier parts of western South Africa and Namibia. Initial research (Foden et al., 2007) suggested that there was strong evidence that a developing range shift in this species reflected a "fingerprint" of anthropogenic climate change. Using a Thornthwaite index of evaporation for the region, researchers interpreted the pole- to equatorward increase in mortality as a result of the critical physiological thresholds being exceeded as a result of the increase in temperature in the region since 1970. This result was widely reported in the scientific and popular literature (e.g. Joubert, 2006).

However, a recent study suggests that the greatest mortality in the species has occurred in the middle of the species range and not at the equatorward extreme (Jack et al., 2016). Mortality appears not to be driven by recent changes in climate (i.e. temperature-linked indices of water balance) and the population dynamics of this species is influenced by episodic recruitment and mega-drought events such as those recorded in the 1940s and 1950s. Changes in climate over much longer time frames, such as the Holocene, also have important implications for the expansion and contraction of the distribution range of this long-lived species where individuals can live for 200 or more years. The importance of windthrow under conditions of high wind and moist soils has also been raised as an important determinant of mortality which

Fig. 7. Eagle Siding near Kei River, former Transkei (No. 548). Savanna biome. There has been a rapid and almost complete conversion of old lands in the early photograph to tall shrubs and trees typical. Such extensive conversion is relatively common throughout much of the coastal platform in the eastern part of South Africa. [A (top): Edwards, 26 December 1954; B (bottom): Puttick and Hoffman, 13 August 2010].

can contribute as much as 70% to the mortality of adult plants in some populations (Jack et al., 2014).

5. Concordance or conundrum? Possible reasons for mismatches between historical trajectories and future projections

In this study, we show how trends in long-term historical data sets can help to contextualize and re-frame the generally catastrophic environmental narratives about the future by providing a more realistic insight into the resilience of southern African biomes in the face of over a century of recorded climate change. Our understanding of how environments have changed in the past is evolving and is likely to change in the future in response to changes in local and global drivers (Stevens et al., 2015). The degree of continuity between historical changes and projected trends can also help in navigating the uncertainty surrounding the impacts of climate change on ecosystems. In some instances, such as in the savanna areas of the eastern seaboard of South Africa, there is reasonable agreement between historical trajectories and recently proposed projections for the future, although significant differences still exist in the details over the nature, timing and extent of change. Woody thickening within the Savanna biome itself might have occurred significantly earlier and at a faster pace than anticipated by the models. In other instances, however, such as in southern Namibia or in the Grassland biome, findings from long-term historical studies suggest that the direction of change over the last several decades has been fundamentally different from that which is expected to occur in the future, at least according to some model outputs. We suggest four reasons why such differences between historical trajectories and future projections might occur.

a *Models and projections do not adequately represent the key drivers and processes of the environment and how they might interact.* Species associations with the environment are extremely

complex and are influenced by climate, soils, land use, disturbance, biotic interactions and demographic processes amongst many other variables (Huntley et al., 2010). Creating a realistic model of these influences is difficult and subject to numerous assumptions at many levels. Historical observation, on the other hand, integrates these influences and it is possible to provide a relatively accurate measure of the extent, nature and rate of change in key environmental components over historical time frames. Although it is often difficult to separate out multiple influences on these observed changes, the documentation of repeated patterns across long environmental gradients is often helpful in this regard. Furthermore, comparison of adjacent areas of different land use can help in distinguishing the effects of land-use and climate, because adjacent sites can be assumed to have experienced the same changes in climate.

b *Climate patterns are still within the 'normal' bounds of variation and / or critical physiological thresholds have not yet been exceeded*. Despite the relatively large increase in temperature in southern Africa over the last few decades the physiological conditions for most plants are not yet severe enough to result in significant changes in phenology, growth, reproduction and recruitment which can be measured at appropriate spatial and temporal scales. Therefore, the radical changes in the environment, portrayed by some of the models, might only become evident once ecological thresholds are crossed. It follows, however, that if future environmental conditions are likely to be so different from anything experienced in the last millennium then an understanding of historical vegetation trajectories will not be helpful in a no-analogue future (Williams and Jackson, 2007).

c *Species responses to climate change are complex and time lags are inevitable*. The adults of many long-lived organisms, such as *Acacia erioloba*, *A. mellifera* or *Aloe dichotoma* can persist in the landscape for decades and survive adverse conditions that are not conducive to the recruitment of new individuals into the population. For semi-arid southern African this is a particularly important consideration as the influence of episodic high rainfall events (Joubert et al., 2013) and mega-droughts can influence the population dynamics of key species for decades into the future. The projections from bioclimatic envelope models match current distributions with present day environmental parameters and thus do not consider that present day distribution of long-lived species may instead reflect conditions that prevailed decades or even centuries ago at the time of their recruitment (Millar and Woolfenden, 1999).

d *Long-term historical data (including repeat photography) are patchy and/or incomplete*. In many instances historical measurement of environmental change is based on only two or a few time steps for a relatively small number of sites. It is often not possible from such a limited data set to gauge the complex trajectories that inevitably characterise a broader region that has been subjected to multiple influences over long time scales. Seasonal effects and short-term cyclical responses also need to be thoroughly considered in the interpretation of long-term historical information. Repeat photographs usually reflect local to landscape levels of scale and the changes observed in the photographs are, therefore, more likely the result of local processes rather than regional changes in climate. In most studies, the limitations of historical data sets are not explicitly stated (Pooley, 2018).

6. Conclusions

Our studies of repeat photographs suggest that significant differences exist between modelled projections and observed measurements of vegetation change. For most southern African biomes, there is little evidence yet of the catastrophic shifts in ecosystem structure and function envisaged for the future. Despite increasing temperatures, most biomes appear relatively stable on decadal time scales, or show increasing vegetation cover and biomass. The desert biome has not expanded into large parts of the Succulent Karoo biome nor has the Nama-karoo biome extended its range into the more mesic Grassland biome. In the Savanna biome, where the greatest change has occurred, the significant increase in woody plant cover has been a characteristic and dynamic feature of this region for decades.

Overall, the discrepancies between models and observations are generally in the direction of a less severe impact than expected based on climate projections and modelling experiments. Some biomes are recovering from past over-exploitation and others are regenerating following a reduction in livestock numbers and the abandonment of agricultural land. Still others appear resilient to the warming trends that have been experienced thus far. This is not to underplay the potential seriousness of future climate change, which may in the future exceed ecological resilience. It does, however, point to a less catastrophic interpretation of environmental change in southern Africa, and highlights the importance of past land use as a driver of the changes in the environment that are evident today. At the very least, the nature, extent and rate of vegetation change derived from historical perspectives provides a useful context within which to evaluate future projections for the subcontinent. Such a past-present-future perspective also identifies appropriate land use practices which could best influence future environmental trajectories.

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